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THE EFFECTS OF FACTORS IMPORTANT IN SEMI-ARID ENVIRONMENTS ON THE EARLY DEVELOPMENT OF *UCA SUBCYLINDRICA*[1]

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ABSTRACT

Lack of food and salinity extremes are conditions encountered by the early life stages of *Uca subcylindrica* in their semi-arid habitats, where nursery areas are temporary rainfall puddles. Several characteristics of the larvae and early postlarvae promote high survivorship in these extreme environments. When starved, yolk reserves in the two zoeal stages lasted through metamorphosis to the megalopal stage and allowed ≥50% survival for 11 days after that. Food was required by the megalopae, however, before molt to crab I occurred. Larvae and early postlarvae survived and developed in a wide range of salinities under laboratory conditions—0.08 to ~50‰. The ability to hyperosmotically regulate the blood was present at hatch. Tolerance to higher salinities increased with successive stages as the ability to hypo-osmotically regulate improved. The early stages of other fiddler crab species are unlikely to survive and develop in the conditions experienced by the zoeae, megalopae, and early crabs of *U. subcylindrica* in their unusual habitats.

INTRODUCTION

Early development of *Uca subcylindrica* is unique among the Ocypodidae in that larval development is completed with only two brief, maturationally advanced zoeal stages. Metamorphosis occurs within 2 to 3 days of hatch, producing morphologically and behaviorally advanced megalopae. First crabs may appear within 4.5 days of hatch but average 8 days. This abbreviated development is critical since the early stages develop in temporary rainfall puddles which last only a few days (Rabalais and Cameron, 1983). Besides a restricted time for development, the early stages of *U. subcylindrica* also face salinity extremes due to high evaporation and sporadic heavy rainfall in their semi-arid habitats. Larval and early postlarval stages have been collected in the field from water ranging from fresh up to 65‰ salinity (Rabalais, 1983). Finally, suitable food is limited in these temporary puddles.

The effects of salinity and nutrition have been studied in the early life stages of several decapod crustaceans but seldom in species with abbreviated development. Rabalais and Gore (1985) compared closely related species with different developmental sequences and found that those with abbreviated development benefited from higher survival rates than those with more prolonged planktonic existence. Most authors point to degrees of lecithotrophism as the overriding advantage of abbreviated development. Several characteristics, including stored food reserves, appear to be im-

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portant in the high survivorship of early stages of *Uca subcylindrica*. We therefore conducted experiments to test the effects of selected ecological factors on survival and development of larval and early postlarval *U. subcylindrica* and to record the physiological responses of successive stages to salinity.

Materials and Methods

Maintenance of ovigerous females and cultures

Ovigerous females were collected from Santa Gertrudis Creek, Kingsville, Texas. Females with late-stage eggs (Rabalais, 1983) were held in large fingerbowls with 2 cm of 15‰ salinity water and would usually release zoeae within a few days. Females with early- or mid-stage eggs were placed on moist (with 15‰ salinity water) paper toweling in a darkened jar, and hatching occurred within 9 to 24 days. Separate broods were designated by letters.

Only vigorously swimming, healthy-appearing zoeae were used. Larvae and early postlarvae were offered freshly hatched *Artemia salina* nauplii daily, except in starvation experiments. Unless noted otherwise, cultures were maintained under a 14L:10D photoperiod, 26°C, and 15‰ salinity. No antibiotics or fungicides were used. Cultures were counted at 24-h intervals for live individuals of each stage; exuviae and dead individuals were removed and preserved.

Salinities from 2 to 65‰ were prepared by dilution of natural sea water with deionized water or by concentration with artificial sea salts (Instant Ocean). A single exception is noted below. Artificial pond water (0.5 m*M* NaCl, 0.4 m*M* $CaCl_2$, 0.2 m*M* $NaHCO_3$, and 0.05 m*M* KCl) gave a salinity of 0.08‰. Salinity was checked daily, readjusted as necessary, and water changed every two days.

Treatment of data

Survivorship and development curves were plotted for each culture as in Figure 1. Data considered "landmarks" were obtained from these graphs and included percent survival of all individuals of all stages, percent surival to the megalopal stage, percent survival to the crab I stage, time required for 50% to reach a particular stage, and intermolt duration, number of days required for 50% of the individuals at a particular stage to attain the next stage. Development times were secondarily derived from the graphs at intersections of the percent and time scales and represented values of ±0.1 day. Data are presented as means ±S.E. derived from replicated group cultures. Differences in survival and development times were tested by analysis of variance (one way) and analysis of covariance (one way). Differences in blood osmolality values and sizes of individuals in the starvation experiments were tested by *t*-Tests.

Variability among broods

Because the number of larvae per female was relatively small (Rabalais and Cameron, 1983), several broods were used. The variability among broods was studied using 4 different broods reared in 15‰. Five replicates of 20 individuals each from brood B were reared in 250-ml fingerbowls; 2 replicates of 25 individuals from brood C, in 500-ml fingerbowls; 10 replicates of 12 individuals from brood D, in 200-ml containers; and 4 replicates of 15 individuals from brood E, in 250-ml containers. The volume per larva ranged between 12.5 and 20 ml.

Effects of starvation

Five cultures of 20 larvae each were starved. Exuviae and dead individuals were removed immediately so that they would not become food. Cultures were held in 250-ml fingerbowls for 24 days. Brood B (Fig. 1) served as the control culture of fed individuals.

Additional cultures of approximately 75 individuals were maintained along with both the fed and starved replicate cultures. To test for the effect of starvation on size, individuals were removed from these cultures and preserved at recorded intervals. Carapace lengths of zoeae were measured laterally from the base of the rostrum to the most posterior margin. For megalopae, carapace width was measured at the greatest distance across the carapace.

When survivorship began to decrease significantly on day 12 (t-Test, $P \leq 0.05$) in replicated starved cultures, the starved mass culture was divided, with feeding resumed for half the individuals and starvation continued for the others (n = 24 individuals per condition), for 12 more days.

Effects of salinity

The effects of salinity on survival and development were assessed in two series of experiments. In the first, 2 replicates of 25 individuals each from brood C were held in 500-ml containers and acclimated in 5‰ steps of 0.5 to 1 h duration to final salinities of 0, 2, 15, 25, 35, 45, and 55‰. In the 45‰ culture for brood C, the salinity rose to 50–51‰ on day 2; thus the development for brood C more closely represented ~50‰, at least initially, and is designated as such. From brood E, a second series of 10 replicates of 12 individuals each in 200-ml containers were acclimated in similar fashion to 2, 5, 15, 25, 35, and 45‰. Five replicates of 20 individuals in 250-ml containers were also acclimated from this brood to 0.08‰.

Osmoregulation in the early stages

For these experiments, water (except 0.08‰) was prepared with artificial sea salts and dechlorinated tap water. Cultures were maintained under a 12L:12D photoperiod and 25°C. Zoeae I were acclimated to 0.08, 2, 5, 30, and 45‰ from 20‰ by 5‰ increments over 0.5 to 1 h intervals, and maintained at the final salinity for 4 h prior to sampling. If the time period was extended much longer, many of the zoeae I would be molting to zoeae II. Results of previous larval studies have shown that the acclimation time for step-wise salinity changes is approximately 1 h, as judged by the period required for body fluids to reach osmotic equilibrium (Foskett, 1977; Young, 1979; Russler and Mangos, 1978). Some zoeae II which survived in 45‰ salinity were acclimated to 55‰ and sampled 1 day later. Because survival was reduced by the megalopal stage at the extremes of salinity, megalopae and crab I individuals reared in 2‰ were acclimated to 0.08‰ and sampled 1 day later. Step-wise acclimations were also made on megalopae and crab I individuals reared at 15‰ up to 45‰ and those reared at 30‰ up to 55 and 65‰ and sampled 1–3 days later. To avoid possible changes in blood osmolality associated with ecdysis as found by Kalber and Costlow (1966), but not by Foskett (1977), samples were taken approximately midway through stages. A few unhatched, late-stage embryos which were dropped from the broods of two females were also sampled.

Blood sampling followed the techniques of Foskett (1977). A larva was removed from the rearing medium, caught in an oil-filled, funnel-shaped glass trap, and blotted

free of excess water. Under a dissecting microscope, micropuncture and blood sampling was accomplished by inserting an oil-filled micropipet through the epithelium between the posterodorsal edge of the carapace and first abdominal somite and into the cardiac area. Postlarvae, which did not conform to the glass traps, were held immobile at the frontal region of the carapace with finely pointed forceps. Approximately 10 nl of the 20 to 80 nl blood sample aspirated was delivered to an oil-filled sample chamber of a direct reading nanoliter osmometer (Clifton Technical Physics). Samples as small as 1 to 10 nl could be analyzed with a reproducibility of ±10 mOsm/kg. Blood osmolality was usually determined immediately, but could be determined as long as 20 or 30 min later without change in the freezing point depression. Samples of the medium were taken concurrently and their osmolality (±3 mOsm/kg) determined on a vapor pressure osmometer (Wescor Model 5130) within 0.5 days of sampling. Both osmometers were calibrated with the same osmolality reference standards. Readings between the machines did not vary more than the error of measurement in the nanoliter osmometer.

Results

Variability among broods

Inter-brood variability (Fig. 1) was statistically significant, but due entirely to brood E, which had a high mortality rate in zoeae II and poorer survival at the megalopal state ($P \leq 0.05$) and at the crab I stage ($P \leq 0.01$). The lower survival of brood E was also apparent in the later salinity series (Fig. 4). Brood E also had shorter intermolt durations in the megalopae ($P \leq 0.001$) and in crab I individuals ($P \leq 0.01$) (Fig. 1). Except for this one brood, there did not appear to be any substantial variation in survival or developmental timing among different broods. There was a statistically significant ($P \leq 0.05$) difference in the intermolt duration for megalopae among broods B (5.1 ± 0.1 days), C (5.0 ± 0.0 days), and D (4.2 ± 0.3 days), but these small differences were probably related to slight differences in the timing of counts and the rapidity of the first zoeal stage. Brood D reached crab I stage significantly faster ($P \leq 0.001$), but the difference disappeared by the crab II stage.

Effects of starvation

Survivorship did not differ between fed and starved larvae until day 14 (*t*-Test, $P \leq 0.05$) (*cf.* Figs. 1, 2A), although a precipitous decline in survivorship in starved cultures began between day 11 and 12 (*t*-Test, $P \leq 0.05$). In fed cultures, development proceeded into crab IV by day 22 (Fig. 1, Brood B). In starved cultures, development proceeded through zoea I and II and into the megalopal stage, and followed essentially the same timing and pattern as fed cultures through day 6 (Fig. 2A), but molt to crab I did not occur.

Size differences in starved and fed larvae (zoeae II) and megalopae were not evident on days 2, 4, or 6. By day 14, when survivorship fell significantly, starved megalopae were smaller than starved megalopae on day 6 (*t*-Test, $P \leq 0.05$). When feeding was resumed on day 12 in cultures which had been starved, survival leveled off (Fig. 2B). When feeding was resumed, molt to crab I occurred within 3 days and development proceeded to crab III by day 23 (Fig. 2C), or within 12 days of refeeding.

Effects of salinity

Larvae and early postlarvae survived and developed through a wide salinity range—0.08 to ~50‰ (Fig. 3). There was 100% mortality within 24 h for larvae in 0‰ and

within 36 h in 55‰. No zoea I molted at these extremes. The effects of salinity on survival for megalopal and crab I stages for broods C and E are summarized in Figure 4. Mean survival to megalopa was significantly lower in 0.08‰ than in 2‰ ($P \leq 0.05$) but still high. Between 0.08‰ and 35‰, survival to megalopa averaged 82% for both series. In the ~50‰ cultures, survival was significantly lower than in the 45‰ cultures ($P \leq 0.001$) but leveled off when salinities were returned to 45‰. Mean survival to crab I was significantly lower at 0.08 to 2‰ within the E series than at the other salinities ($P \leq 0.05$) (Fig. 4). Still, mean survival to crab I ranged between 55 and 85% for most cultures between 2 and 45‰ and did not fall much below this in 0.08‰ (Fig. 4). Survival to crab I was below 20% in the ~50‰ cultures and differed from that in the 45‰ cultures ($P \leq 0.05$) for reasons discussed earlier. In most cultures at most salinities (Fig. 3), mortality was usually greater in the second zoeal stage and during metamorphosis to megalopa. After attainment of megalopae, survivorship leveled off, with highest mortality during molting.

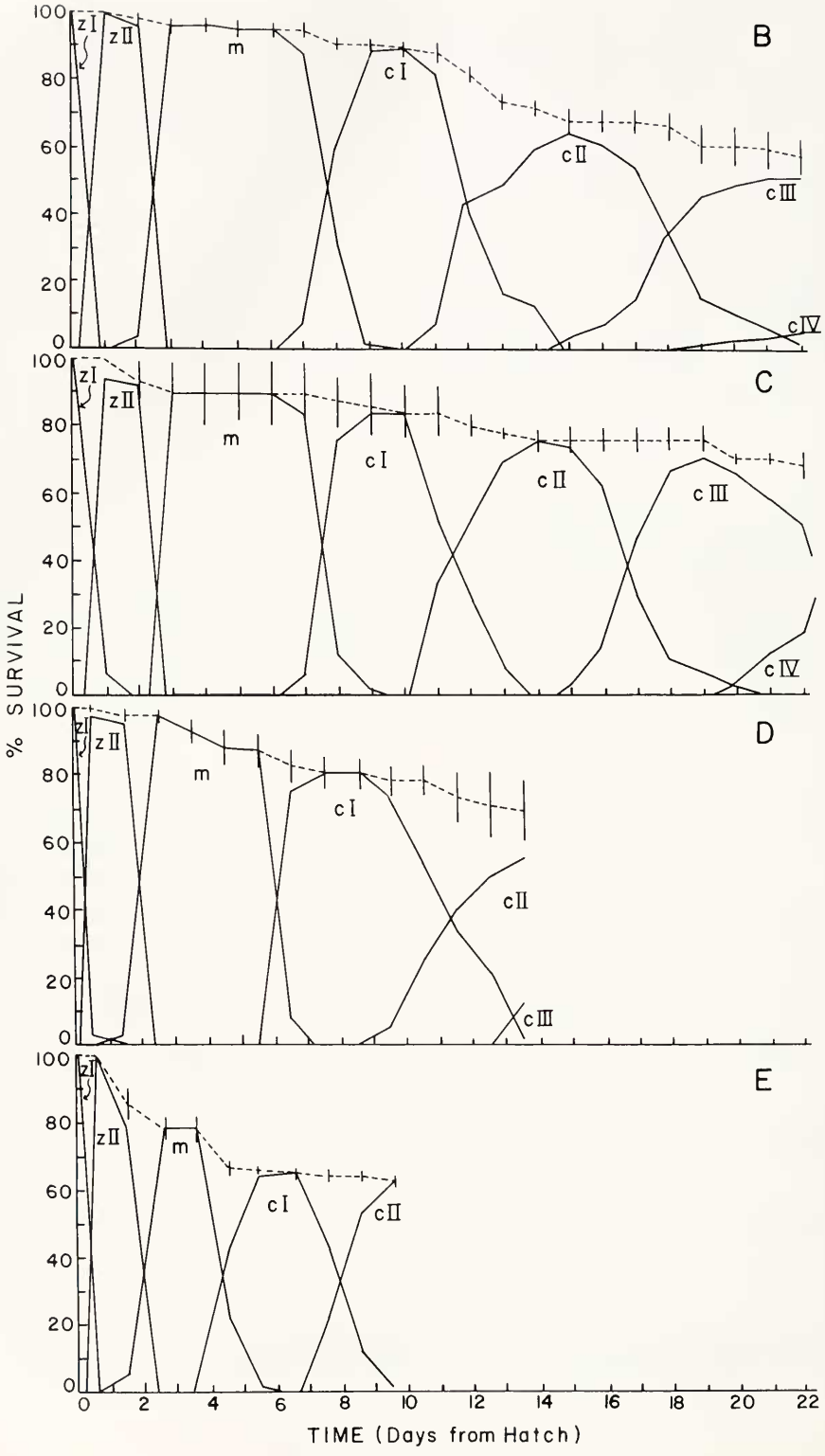
Any effect of salinity on development time was not obvious. Analysis of covariance showed differences between the C and E series across salinities in intermolt duration for zoeae II ($P \leq 0.001$) and in intermolt duration for megalopae ($P \leq 0.001$). Differences in intermolt duration for zoea I were incalculable (no deviation around the means in the E series) and were insignificant in crab I. In another analysis of covariance between the two series, there were differences between C and E in time for 50% of the individuals to attain crab I ($P \leq 0.01$) and crab II ($P \leq 0.01$) but not megalopae ($P > 0.05$). Because of the variability shown between these two series, analyses of variation in development times along a salinity gradient were computed within each series. Although not always significantly longer, there was a tendency for prolongation in development time at the higher and lower salinities, within each series. Optimal development times were seen mostly in the 5, 15, and 20‰ salinity cultures.

Osmoregulation in the early stages

Zoeae I hyperosmotically regulated over 0.08 to 45‰ salinity with the strongest gradient at the lowest salinities (0.08, 2, and 15‰) (Fig. 5). Zoeae II also hyperosmotically regulated over the same salinity range (Fig. 5). Blood osmolality of zoeae II held at 30 and 45‰, however, was only slightly higher than the medium. Zoeae II survived in 55‰ where there was a tendency towards hyporegulation of blood osmolality.

In the megalopae (Fig. 5), values for shorter *versus* longer acclimation times did not differ except for those at 2‰ ($P \leq 0.05$) and at 45‰ ($P \leq 0.02$), but the number of values for these comparisons was low. These differences were also not consistent across salinities or the period of acclimation. The gradient between the blood and 0.08‰ salinity was greater in the megalopae than in zoeae II, as was the reversed gradient at the higher values of 45 and 55‰ (Fig. 5). The isosmotic point was 40‰. Megalopae survived and hyporegulated at 65‰, whereas zoeae II did not survive. Some megalopae in 65‰ were covered with bacteria, and most remained listless on the bottom of culture dishes.

For crab I individuals (Fig. 5), in only one instance did the time of acclimation affect blood osmolality values. At 45‰, mean blood osmolality values for those acclimated 1 day from 15‰ differed from those acclimated 2 days and from those reared in 45‰ ($P \leq 0.001$), but the latter two did not differ significantly. The osmoregulatory pattern for crab I individuals differed from that of megalopae (Fig. 5); there was a larger gradient between the blood and medium at 45‰, and a lower isosmotic point (~30‰).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Osmolality values obtained from 4 late-stage embryos which fell from egg masses onto moist paper toweling or into water of 20‰ (630 mOsm/kg) 2 to 4 days prior to hatch of the remainder of the brood averaged 947 ± 4 mOsm/kg.

Discussion

As a subject for these studies, *Uca subcylindrica* presented both advantages and difficulties. The ovigerous females were difficult to collect because of their seasonal reproductive activity and secretive habits and, thus, were limited in number. They also have relatively few eggs, which imposed a limit on replication. On the other hand, their relatively large and distinctive larval and postlarval stages greatly facilitated the assessment of survival and developmental stages. Maintenance of the early stages was also easy, since yolk reserves sustained them well into the megalopal stage, when they were easily fed. Their lecithotrophic nature also eliminated cannibalism as a problem for mass cultures (Dawirs, 1982). Although the use of mass cultures does not allow exact age determination for each individual, as recommended by Dawirs (1982), there was sufficient synchrony in the replicates (*e.g.*, Figs. 1, 3) to allow accurate determination of developmental "landmarks" for comparison by several statistical techniques.

Variability among broods

With the exception of one anomalous brood, variability among broods in survival was insignificant and in development time was minimal. Within a brood, variability was also minimal (0.5 to 1 day) as shown by consistent development times and intermolt durations seen in the two salinity series at 5 to 25‰. The single anomalous brood where differences approached 2 days in intermolt duration and the minimal differences among the others support the findings of Provenzano *et al.* (1978) and Sandifer and Smith (1979) that genetic or other quality variations among broods of larvae may account for significant variation in larval duration and/or survival. Lack of variability cannot be considered a truism for species with abbreviated development (*e.g.*, Dobkin, 1963; Fielder, 1970), at least for *Uca subcylindrica* (data presented here and in Rabalais and Cameron, 1983), and this variability should be considered when studying effects of laboratory manipulations. Differences, however, were small, and effects outside this range could be attributed to experimental treatments.

Effects of starvation

Zoeae of *Uca subcylindrica* are lecithotropic, *i.e.*, they hatch from large, yolky eggs and use stored yolk as energy for growth and metamorphosis rather than relying on planktonic prey. Yolk globules are retained as a mass beneath the carapace in both zoeal stages and the megalopae (Rabalais and Cameron, 1983). These yolk reserves are apparently sufficient for development into the megalopal stage, but molt to crab I will not occur without food (Fig. 2). Accessory setae are reduced or absent on feeding appendages of the zoeal stages (Rabalais and Cameron, 1983). On the

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FIGURE 1. Inter-brood variability in survival and development as shown in four different broods (B–E) reared at similar conditions of temperature (26°C), salinity (15‰), and photoperiod (14L:10D). Values for stages are means of the replicates. Total survival of all individuals ±S.E. plotted across the top of the stages with a dashed line. Roman numerals denote stages; z = zoea, m = megalopa, and c = crab stage.

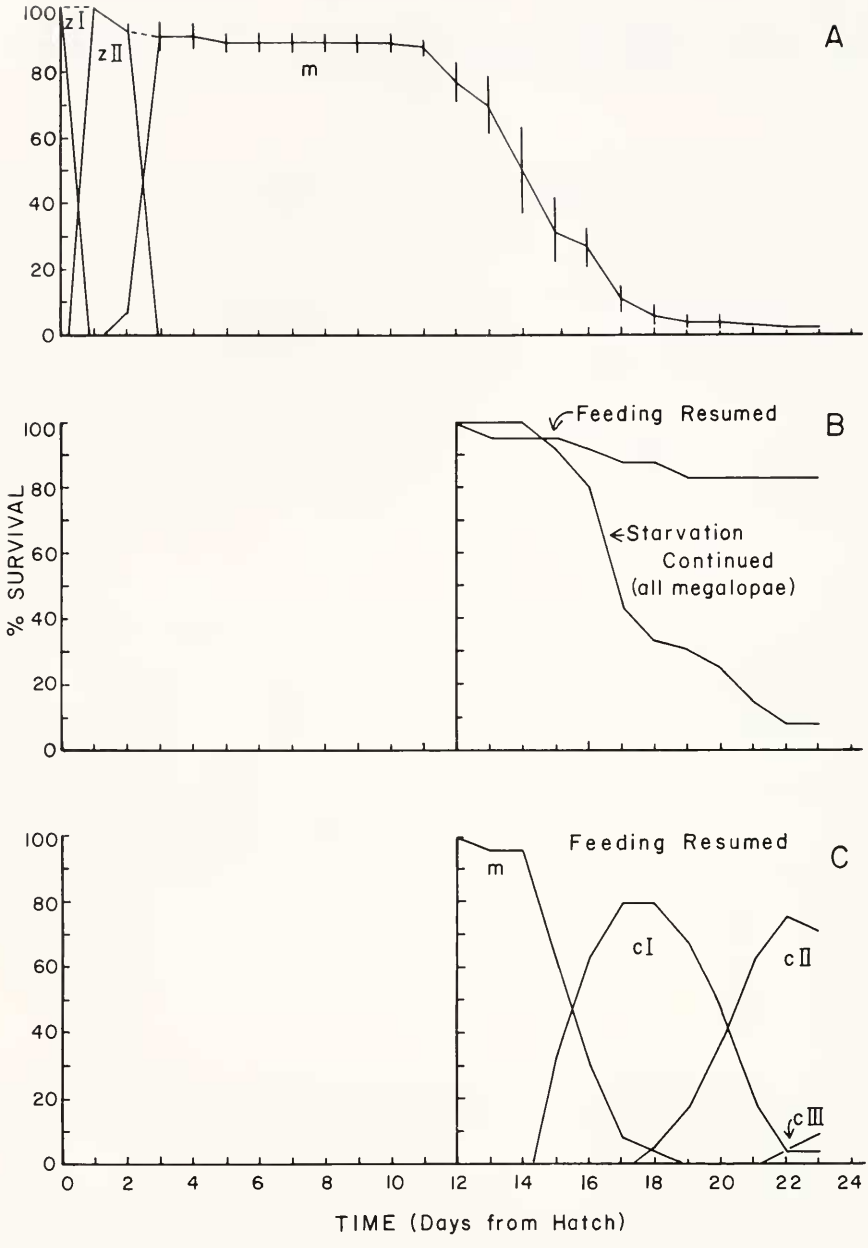

FIGURE 2. A. Percent survival and development for starved cultures at 15‰, 26°C, 14L:10D photoperiod. Values are means of 5 replicates of 20 individuals. Total survival of all individuals ±S.E. plotted across the top of the stages with a dashed line. B. Percent survival of all individuals of all stages for the starved culture in which feeding was resumed for half the individuals and starvation was continued for the other half (n = 24 each). C. Percent survival of the individual stages and development for the 24 individuals in which feeding was resumed after 11 days of starvation. Roman numerals denote stages; z = zoea, m = megalopa, c = crab stage.

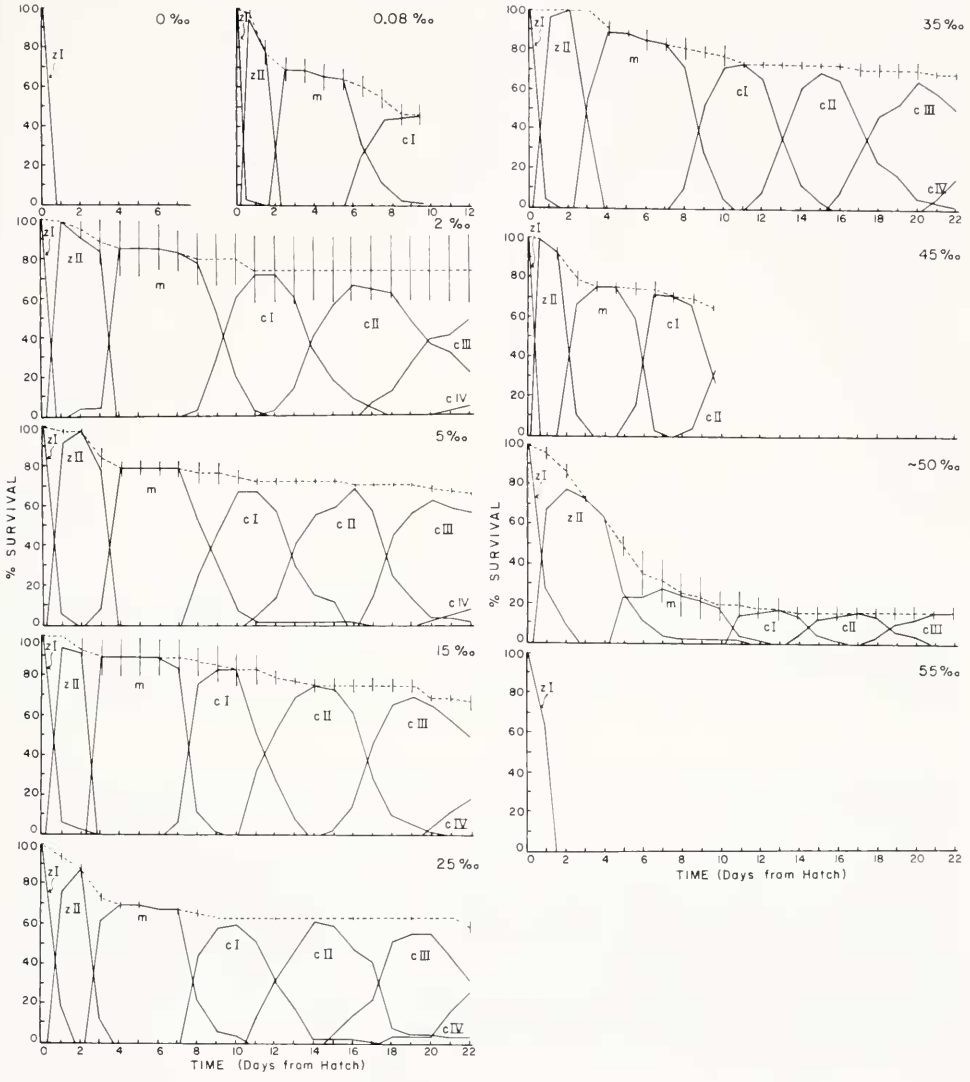

FIGURE 3. Survival and development for larvae and postlarvae reared at various salinities shown at upper right in each panel. Animals at 0.08 and 45‰ from brood E; the rest from brood C. The ~50‰ was 50–51‰ in the initial stages then 45‰. Data presented as in Figure 1.

other hand, feeding appendages of the megalopae are notably more setose with a greater variety of setae than other described *Uca* megalopae, a condition more typical of a first crab. Feeding behavior is consistent with these morphological features. Zoeae would not take food (*Artemia* nauplii, rotifers, and other *Uca* zoeae I) which was offered but the megalopae were voracious feeders and actively swam after, captured, and consumed live *Artemia* nauplii. Early crabs were also active predators. Both megalopae and early crabs scavenged dead organisms.

In brachyuran crabs, energy reserves are usually not sufficient to allow development during starvation, and there is a particularly critical period in the beginning of larval

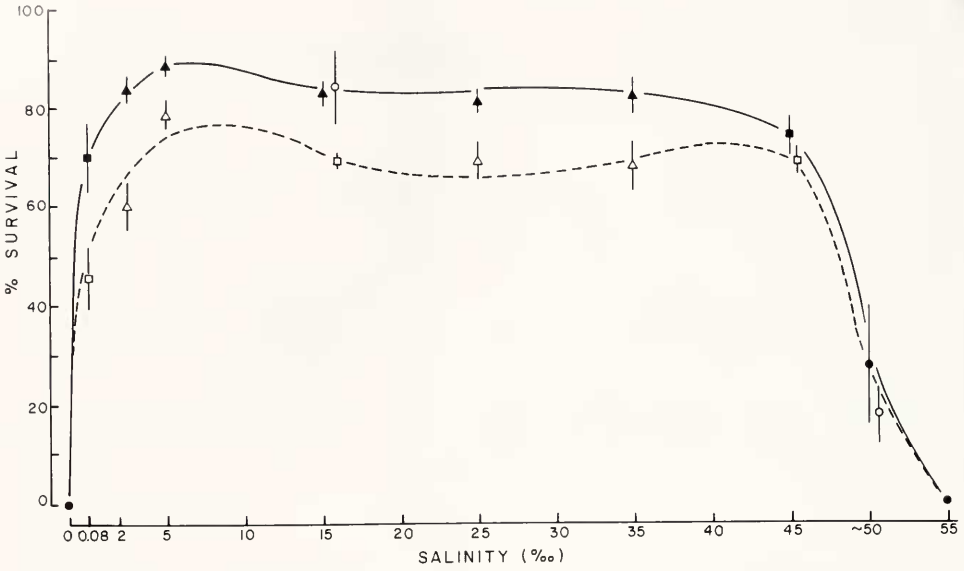

FIGURE 4. Summary of survival data for megalopae (darkened symbols) and crab I individuals (open symbols) from Figure 3. Triangles represent the means of values for broods C and E which were not significantly different. When different, the C series are shown as circles and the E series as squares. Values at 0.08 and 45‰ are brood E (squares) and at ~50‰ are brood C (circles). Salinity axis not to scale at the lower values. Distribution curves (solid line for megalopae and dashed for crab I stages) approximated.

development beyond which starvation may cause irreversible damage to a hormonal or enzymatic system controlling molt (Anger and Dawirs, 1981; Anger *et al.*, 1981). The time when 50% of the starved larvae could not recover when being refed (Point of No Return, PNR_{50}; Anger *et al.*, 1981) was not determined but was obviously longer than the approximately 1 to 2 days for planktotrophic larvae. Megalopae of *Uca subcylindrica* recovered with only 4.2% mortality when feeding was resumed after 12 days of starvation. We estimated that the PNR_{50} occurs between day 14, when survivorship fell below 50% and size differences were noted, and day 18, when listless behavior of megalopae was observed.

Effects of salinity

Some euryhaline crabs have a wide range of salinity tolerance during early development: 10 to 40‰ for *Sesarma reticulatum* (Foskett, 1977), 5 to 40‰ (but with poor survival in 5‰) for *Clibanarius vittatus* (Young, 1979), and 2.5 to 40‰ (but with poor survival at the extremes) for *Rhithropanopeus harrisii* (Costlow *et al.*, 1966). Larvae and early postlarvae of *Uca subcylindrica* survived and developed in a greater range of salinities under laboratory conditions—0.08 to ~50‰—than recorded for any other decapod crustacean (Fig. 3). In the osmoregulation salinity series, zoeae II survived in 55‰, and megalopae and crab I individuals survived in 55 and 65‰. This range of tolerance in early stages differs from that of adults, which survived (>50%) 2 to 90‰ in long-term salinity experiments (Rabalais and Cameron, in prep.). The inability of the early stages of other *Uca* to survive in salinities less than 15–20‰ or greater than 40–45‰ (Fig. 6) makes them unlikely to tolerate the salinity ranges in the habitats of *U. subcylindrica*.

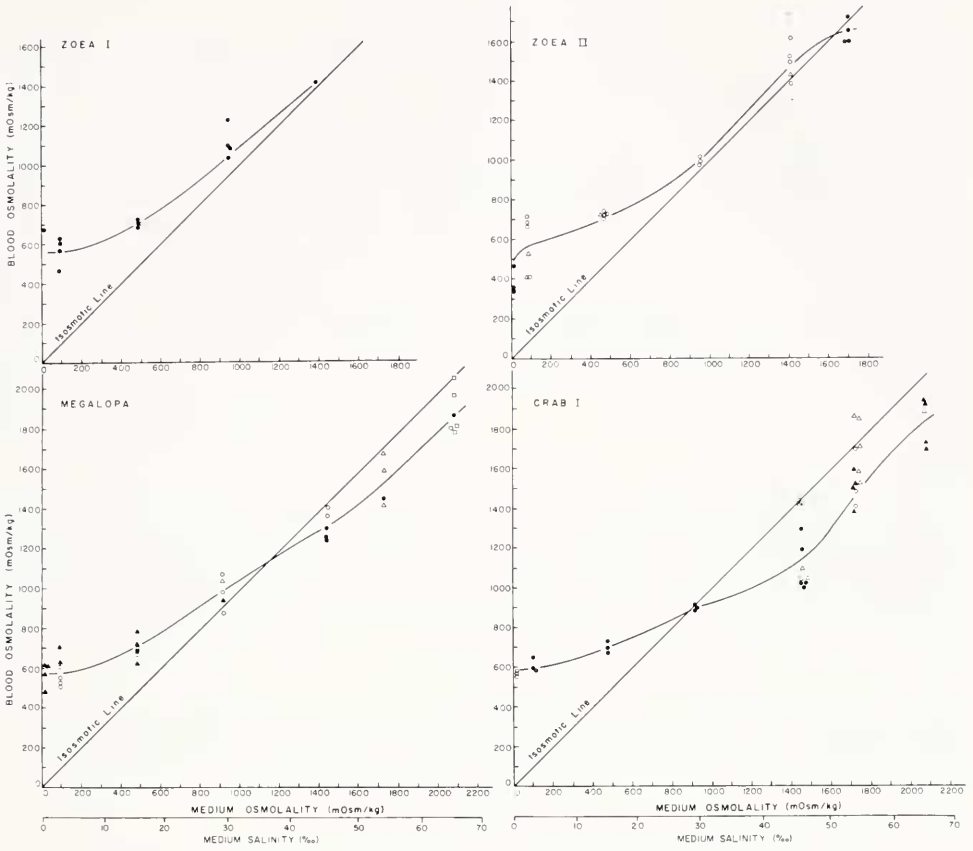

FIGURE 5. Osmoregulation curves for larvae and early postlarvae. Zoeae I from broods G (open circles) and H (closed circles), 6.5–12 h old. Zoeae II from brood H (triangles), brood I acclimated 12 h (open circles), and brood I acclimated 1 day (closed circles). Megalopae from brood G, 7 days old (open circles); brood G, 8 days old (closed circles); from brood G, 9 days old (open triangles); brood H acclimated 1 day to lower salinities (closed triangles); brood I acclimated 1 day to higher salinities (open squares); and brood I acclimated 2 days to higher salinities (closed squares). Crab I individuals from brood F acclimated 10 days (closed circles); brood F acclimated 1 day at the lower and higher salinities (open circles); brood H acclimated 3 days in 55‰ and 1 day in 65‰ (closed triangles); brood G acclimated 2 days at the higher salinities (open triangles). Curves drawn through the mean for each salinity, with the exception of 45‰ in crab I which includes only the lower values (open triangles and closed circles). Approximate salinity values given on second abscissa below medium osmolality.

Tolerance of early stages of *Uca subcylindrica* to a wide range of salinities would be a decided advantage in the habitats in which they are known to develop. To date zoeae I have been found in natural nursery areas with salinities from fresh water to 33‰; zoeae II, in salinities from 2 to 65‰; and megalopae in fresh water to 42‰ (Rabalais, 1983). These values correspond to salinity tolerances in the laboratory (Fig. 3), except for zoeae II in 65‰. The highest value at which zoeae II were found to survive in the laboratory was 55‰, where there was slight hypo-osmotic regulation (Fig. 5), and it is reasonable to expect that survival at 65‰ may occur. Zoeae II which survive in 65‰ may not be able to metamorphose to megalopae at this salinity. Megalopae may only be found in the field at such high salinities if the preceding

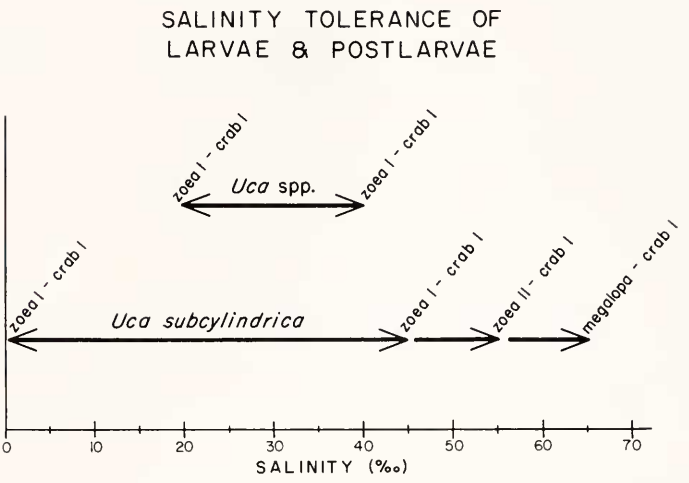

FIGURE 6. Salinity tolerance of larvae and early postlarvae of closely related species—one with abbreviated development, *Uca subcylindrica*, and other *Uca* with longer-developing larvae. Data for *Uca* species from Dietrich (1979) on *U. pugilator*, which did not survive in <20‰ or >40‰ and from personal observations for *U. panacea*, *U. longisignalis*, and *U. rapax* zoeae I, which did not survive in <15‰ or >45‰ (Rabalais, 1983). Horizontal arrows represent limits for survival and development at various salinities for the stages shown. Lower limit for *U. subcylindrica* was a pond water mixture of 0.08‰.

zoeal stages molted at a lower salinity before the effects of temperature and evaporation created higher salinities for the subsequent megalopae.

Osmoregulation in the early stages

Foskett (1977), who studied *Sesarma reticulatum* and reviewed what was known of larval osmoregulation in brachyuran crabs, found that osmoregulation patterns did not change between successive stages. Young (1979), who studied an anomuran hermit crab, supported this finding. On the other hand, Read (1984) reported noticeable changes in osmotic responses between larval and postlarval stages of a palaemonid shrimp. Foskett (1977) also noted that there was no consistent osmoregulatory pattern across a diversity of brachyuran crab species and that there was no clear trend toward development of adult osmoregulation capabilities at the end of larval life (which included megalopae in his consideration). Osmoregulation patterns of the early stages of *Uca subcylindrica* did differ from stage to stage (Fig. 5) and began to approach those of adults by the megalopal and crab I stages. Hyperosmotic regulation in lower salinities by all early stages was similar to adult crabs (Rabalais and Cameron, 1985). On the other hand, a tendency to hypo-osmoregulate at higher salinities began in zoeae II and developed further in megalopae and crab I individuals. The isosmotic point also approached that of the adults by crab I.

The ontogeny of osmoregulation capabilities in larvae and early postlarvae was consistent with the survivorship curves for these stages. For example, in 45‰, the greatest mortality was in zoeae II (Fig. 3) where there was hyperosmoconformity (Fig. 5) and leveled off in the megalopal and early crab stages (Fig. 3) when hypo-osmotic regulation began for this salinity (Fig. 5). Mortality was usually greater in larval stages than in early postlarval stages in most salinities. Combined with results from the salinity tolerance experiments, it is obvious that *Uca subcylindrica* larvae and postlarvae

are surviving in a wide range of salinities as a result of regulation of blood osmolality, not just by conforming to and tolerating the external media.

Several characteristics of the early development of *Uca subcylindrica*, especially the wide range of salinity tolerance, prove advantageous in the semi-arid habitats in which these crabs live. Since ecdyses are critical periods in larval life and highest mortality of cultured decapod larvae often occurs then (Knudsen, 1960; Roberts, 1971), reduction in the number of premetamorphic molts may increase larval survivorship (Sandifer, 1973). The mortality among larvae of several species during this critical period may be related to an inability to maintain an osmotic or ionic gradient at the time of molt. A reduction in the number of molts and their associated physiological stress would be advantageous to species which inhabit more dilute media, are exposed to extremes in salinities, or are incapable of appropriate behavioral responses necessary to avoid suboptimal conditions. Early development of *U. subcylindrica* benefits from both a reduced number of molts and stages which can regulate against lower and higher external media.

In summary, several features of the early stages of *Uca subcylindrica* promote high survivorship in a variety of culture conditions and include the lecithotrophic nature of the larvae and early postlarvae, maturationally advanced morphological characteristics and behavior, a reduction in the number of critical molt periods, and the physiological ability to survive and develop through an extremely wide range of salinities. These factors are important since food shortages and extremes of salinity which would tax any organism are found in their nursery areas. The larvae and early postlarvae of other *Uca* are unlikely to survive and develop under such conditions. Combined with differences in the physiology and morphology of adult crabs (Rabalais and Cameron, 1985), knowledge of the characteristics of the early stages contributes to our further understanding of why other fiddler crab species are not usually found in the semi-arid habitats of *U. subcylindrica*.

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